By 1974 only 130 ha of forest and scrub remained (White and Edmiston 1974). A slightly smaller area remains today, forming mostly scattered relic stands (Figure 3) of the communities which once predominated over much of the island. On the other hand, there is evidence of a limited recovery of *Acacia rostellifera* over the last 30 years, south of Stark Bay, northeast of Wilson Bay and within protective exclosures.

Coastal erosion was recognised by Storr (1965) and White and Edmiston (1974) as a factor inducing vegetation change. In the short term, erosion favours some species associated with the mobile dune environments, and this can lead to an increasingly larger area of the island being exposed to salt spray. Several large blowouts occur on Rottnest Island, the largest of which, Barnett's Gully, has increased substantially in size over the decades (White and Edmiston 1974) while others have fluctuated only slightly.

Despite the fragmentary nature of early accounts, and the qualitative nature of many observations since, a number of clear trends are evident, mostly related to the severe effects of man's interference with the island ecology:

1. Large tree and shrub species, such as *Callitris*, *Melaleuca* and *Acacia*, are declining and mostly failing to regenerate.
2. Some communities dominated by large or small shrubs seem capable of natural regeneration, though they are not vigorously expanding. These include *Templetonia*, *Pittosporum*, *Spyridium* and *Leucopogon*. Given reasonable protection, such plants may be encouraged to extend their areas.
3. *Acanthocarpus*, *Olearia*, *Westringia* and *Trachyandra* are highly successful colonisers of niches left by the destruction of sensitive species.

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Marine biological studies on Rottnest Island

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Abstract

Recent studies on marine invertebrates at Rottnest Island have revealed four main features about animals living on the rock platforms. First, large components of the fauna and patterns of reproduction of individual species are characteristic of more tropical conditions. Secondly, quantitative analyses of observations on natural history and experimental manipulations involving different behaviours, morphologies or microhabitats disclosed the significance of particular traits. Thirdly, biological interactions were powerful determinants of the use of food and space among a group of grazers. Finally, analyses of the genetical structure of populations demonstrated responses to environmental heterogeneities and a previously unappreciated prevalence of asexual modes of reproduction.

Introduction

The Rottnest Island Biological Research Station in the last three decades has been the base for studies on the invertebrate animals living on the rock platforms which surround the island. These studies follow four themes described in the following sections. In combination, these four approaches have revealed a great deal, not only about the benthic marine invertebrates on Rottnest Island, but also about general ecological processes influencing and involving benthic marine animals.

Descriptive biology

The most extensive work has been on individual species of molluscs: basic patterns of growth and/or reproduction are established for the gastropods *Dicathais orbita* (Phillips 1969; Phillips and Campbell 1968, 1970; Phillips *et al.* 1973), *Turbo intercostalis* and *T. torquata* (Joll 1975, 1980, pers comm), and for the sea urchin *Echinometra mathaei* (Pearse and Phillips 1968; Ebert 1982). On the other hand, descriptions of particular faunas are available for isopods on rocky islets (Bunn and Green 1983), for decapod crustaceans inhabiting the coral *Pocillopora damicornis* (Black and Prince 1983) and for fishes (Hutchins 1979).

A striking pattern emerges from these studies: large components of the fauna, and patterns of timing reproduction of individual species are characteristic of the tropics, despite the temperate latitude of Rottnest Island. For example, there are 90 species of tropical fish. As well, local diversity of animals living in *Pocillopora damicornis*, as measured by number of species per unit volume of coral, is as high at Rottnest Island as at some tropical sites. Furthermore, both species of *Turbo* and *Echinometra mathaei* all have continuous rather than seasonal reproduction.

Analyses of ecological processes

These studies involve pairs of interacting species (Black 1978; Chalmer 1974*, Clarke 1975*), analyses of intraspecific morphological differences (Black, *et al.* 1982; Bowen *et al.* 1982*), and analysis of nutrient fluxes (Vink 1982*).

The multi-armed starfish, *Coscinasterias calamaria*, is a generalist predator which feeds on the most abundant species of prey available. When prey density is low, grouped starfish consume a lower number and proportion of prey than when density of prey is high. This behaviour would tend to stabilise the abundance of prey (Clarke 1975*).

The predatory gastropod, *Dicathais orbita* is a major agent of mortality for the limpet, *Patelloida alticostata*. Some 41% of the shells of recently-dead limpets were drilled by this predator. Its tactics, as revealed by the location of the drill holes, are to drill into the gonad and digestive gland, and into segments of the shell where the aperture of the predator's shell fits evenly onto the limpet's shell. This complicated handling of prey provides access to energy-rich tissues and probably prevents dislodgement of the predator (Black 1978).

The ovoviviparous cap limpet, *Hipponix conicus*, lives on other gastropods such as *Turbo intercostalis* and *Campanile symbolicum*. The positioning of the limpet relative to the aperture of the host's shell is critical because the cap limpet consumes the faeces and mucus of the host. Chalmer's (1974*) ingenious experiments demonstrate that limpets adjacent to the aperture of living hosts grow faster and produce more offspring than limpets far from the aperture or on shells without living hosts.

The sea urchin, *Echinometra mathaei*, displays variation in the relative size of components of its skeleton. Black *et al.* (1982) discovered that the size of the food-gathering apparatus, Aristotle's lantern, relative to the diameter of the test, differed between sites with apparently different amounts of food, and among locations with different densities of urchins. These differences suggest that relative or absolute shortages of food are associated with relatively larger Aristotle's lanterns. Experiments by Bowen *et al.* (1982*), clearly showed the adaptive significance of relatively larger lanterns, because these animals consumed more food than urchins with relatively smaller lanterns.

Finally, in a more general approach to ecosystems, Vink (1982*) found that for benthic marine animals the universal application of the Redfield planktonic composition ratio (106 C: 16 N: 1 P) used in the estimation of nutrient fluxes and production, is probably in error, because her analysis of simultaneous CO_2 respiration and excretion of phosphorus gave a C : P ratio of 300 : 1, intermediate between the compositional ratios of plankton and benthic plants.

Distribution and abundance on a steep intertidal gradient

As anticipated by Hodgkin (1960), an extensive series of studies has attempted to discover the causal factors responsible for the observed patterns of zonation of animals on Rottnest Island shores. The emphasis has been on a group of grazing animals living on the 2 metre-high vertical rock walls which form the landward termination of the horizontal rock platforms and which experience steep gradients in both physical and biological conditions (Black *et al.* 1979). The distribution of each of the 11 species overlaps with several others, so there is potential for inter- as well as intraspecific interactions.

Although tolerances to physical conditions on the steep intertidal gradient undoubtedly mould the overall pattern of distribution, biological interactions within and among the species influence the details of this pattern. All three of the mobile grazing gastropods, *Littorina unifasciata*, *L. australis*, and *Nerita atramentosa*, responded to experimental increases in the density of conspecifics by occupying uarger vertical ranges on the shore (Prideau 1976*) This feature too was evident among natural differences in the abundances of conspecifics for *Littorina australis*, *Nerita atramentosa*, *Collisella onychitis*, *Clavarizona hirtosa*, and *Patelloida alticostata* (Ayre *et al.* 1977*). Intraspecific interactions apparently determine the vertical range of distribution of these animals.

Interspecific interactions also affect the patterns of distribution. A summary of results of comparative analyses and manipulative experiments is that *Nerita atramentosa* restricts the vertical extent of distribution of *Littorina australis* (Prideaux 1976*), *Collisella onychitis*, and *Patelloida alticostata* (Ayre *et. al.* 1977*), and *Collisella onychitis* reduces the abundance of *Siphonaria kurracheensis* at mid-shore (Black 1979).

The mechanisms of these interactions among the sedentary, adult stages of these species revolve around both behavioural and morphological features. All the sedentary gastropods occupy home scars and return unfailingly to these scars after excursions for grazing (Ayre *et al.* 1977*; Threlfall 1977*; Black 1977; Austin *et al.* 1979*). This behaviour

* Indicates unpublished Honours thesis, Department of Zoology, University of Western Australia.

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means that individuals can interact only with their most immediate neighbours. In fact, detailed observations of movements of these animals disclosed a very low rate of contacts among neighbours, even though the areas grazed did overlap. The mechanisms of interspecific competition are probably by exploitation rather than by interference, since the items of diet overlap (Turner 1978*), growth rate decreases with increased density of conspecifics (Black 1977, Turner 1978*), and the relationship between average size and density is inverse (Stoddart 1975*, Black 1977).

The basis for the exploitation competition appears to be the structure of the radula. There is great variability in the length of the longest active cusp which scrapes against the rock to remove algae, and these differences do not follow a pattern consistent with the average body size of the species. However, there is a significant positive relationship between the length of the radular teeth and the rate of excretion of inorganic material in the faeces (Ayre *et al.* 1977*, Black, Lymbery and Hill unpublished). The interpretation is that the larger teeth allow grazing not only of the superficial algae but also of the top layer of rock surface, which is impregnated with filaments of algae. For the pairs of species for which the outcome of competitive interactions is known, the species with the larger teeth and greater rate of producion of inorganic material in faeces is the superior competitor. This analysis therefore provides predictions for the outcomes of competitive interactions between pairs of these species not yet experimentally examined, and suggests an approach for analysing interactions among other grazers.

In combination, these studies on distribution and abundance of grazers on the vertical rocky shore demonstrate that biological interactions are powerful organizers of the use of the resources of food and space among members of this guild. Although these interactions involving the sedentary animals seem to have predictable outcomes, a great deal of unpredictability is imposed upon these grazers through extreme variability in recruitment to these populations. Records of recruitment of four species of limpets over 9 seasons show average abundances differing by 2 orders of magnitude from year to year, and even complete failure of recruitment in some years at some localities (Black unpublished). To some extent particular localities are consistently good for recruits in each year, explaining some of the between-habitat differences in the abundances of adults. These data on recruitment emphasize that the essential events of recruitment in these sedentary marine animals are extremely sporadic or patchy in time and space.

Population genetics

Genetic studies of marine animals at Rottnest can be viewed in two contexts. First, the heterogeneity of the marine littoral environment provides a useful situation for the study of localized genetic differentiation. Secondly, population genetics can reveal much about the breeding structure of populations. Electrophoresis of enzymes has allowed detection of genetic polymorphisms in nearly all species examined, allowing a genetic approach to a variety of problems.

The first such study at Rottnest was a comparison of the blue and orange "morphs" of the rock crab *Leptograpsus variegatus*. Earlier work had shown ecological differences between the blue and orange *Leptograpsus* (Shield 1959). Mahon's (1974) electrophoretic study demonstrated the absence of gene flow between these colour forms, indicating that they are in fact separate species.

More recent, and continuing, genetic studies at Rottnest are focussed on the genetic structure of local populations of several species, considering the effects of localized selection and the nature of recruitment. Studies of enzyme polymorphisms indicate that the source of recruits can have a large effect on the genetic mosaicism of local populations.

The vertical rocky shores at Rottnest are dominated by limpets, and two species of the pumonate genus *Siphonaria* have been studied. These limpets produce planktonic larvae which develop into sedentary adults. This common pattern among marine invertebrates poses a conflict between genetic mixing due to planktonic dispersal and genetic differentiation due to localized selection after settlement. Extending Black's (1979) demonstration of bimodal vertical distributions of *Siphonaria kurracheensis*, a study of 5 polymorphic enzymes revealed no differences between high-shore and low-shore populations (Black and Johnson 1981). Contrasting with this absence of a detectable genetic response to the steep environmental gradients in the intertidal zone, there were genetic differences among sites and between adults and recruits. A similar result was obtained for a second, undescribed, species of *Siphonaria*: depending upon the genetic locus examined, genetic differences were found among sites along 50 m of shore, between high and low portions of the shore within sites, between adults and recruits, and between recruits in successive years (Johnson and Black 1982).

Transplant experiments are under-way to determine if these genetic differences are due to localized selective mortality. Such selection is unlikely to provide a simple explanation, however, because the genetic heterogeneity does not follow a simple, consistent pattern, but forms a shifting, ephemeral genetic patchiness. This patchiness results at least in part from temporal variation in recruitment. Over a 2-year period, monthly samples of recruits of the undescribed species of *Siphonaria* were collected from 11 sites around the island (Johnson and Black unpublished). Genetic differences were found among recruits settling at different times. Combined with temporal variation in the distribution and abundance of recruits, this genetic variation gives rise to genetic differences among sites.

These studies of *Siphonaria* indicate that planktonic dispersal, although causing uniformity on a large scale, can give rise to fine-scale genetic patchiness. Large-scale uniformity for the undescribed species of *Siphonaria* has been documented by a study of geographic variation: variation among sites at Rottnest is nearly as great as that among sites from Kalbarri, Western Australia to Port Robe, South Australia. Thus, temporal variation in recruits at Rottnest is not due to differences in source populations. Instead, the variation is correlated with environmental conditions at the time of settlement, implying selective mortality. Since genetic differentiation among areas is often used to delineate stocks of commercial importance, these results for *Siphonaria* are important in demonstrating that the source of such differentiation need not be isolation of populations.

In contrast with the sexually-reproducing *Siphonaria* species, there are many species which utilize asexual reproduction. Genetic studies at Rottnest have been useful in both the detection of asexual reproduction and the assessment of its effects on local populations.

The cherry anemone, *Actinia tenebrosa*, broods young, which subsequently settle near their brood parents. Electrophoretic studies have showed that the young are genetically identical to their brood parents, even when they are heterozygous (Black and Johnson 1979). This absence of segregation indicates asexual reproduction. Similarly, the brooded planula larvae of the coral, *Pocillopora damicornis*, are produced asexually (Stoddart unpublished). This is a startling result, as the production of planulae has always been assumed to be through sexual means.

The effects of this clonal reproduction on the genetic structure of these populations are striking. For both *Actinia tenebrosa* (Black and Johnson 1979, Ayre 1983) and *Pocillopora damicornis* (Stoddart unpublished), there are 1) large departures from Hardy-Weinberg genotypic frequencies, 2) low local diversities of genotypes, as a few clones predominate, and 3) large genetic differences between populations less than 100 m apart. A similar pattern was found for the starfish *Coscinasterias calamaria*, which reproduces by fission (Threlfall 1977*). For *Actinia tenebrosa*, Ayre (1982, 1983) has shown that fine-scale clustering of genetically-identical individuals is facilitated by interclonal aggression, as clones compete for available space.

Each of these species combines sexual and asexual reproduction, as indicated by histological and population genetic studies. Sexual reproduction is apparently used for long-distance dispersal, and is the source of genetic diversity within sites, whereas asexual reproduction contributes to local recruitment. These contrasting modes of reproduction are of interest in two respects. First, there is the theoretically important question of the significance of sexual reproduction; is genetic diversity of offspring beneficial in the colonization of unknown areas? If so, each clone should be selectively favoured in the areas of its establishment. Transplant experiments with *Actinia tenebrosa* have been established, and preliminary results indicate that clones do differ in life history traits, so that the clonal composition in each area may not be simply the result of a planktonic lottery (Ayre unpublished).

The second context in which modes of reproduction are of interest is in the assessment of the importance of local recruitment. The clonal structure of the populations of *Actinia tenebrosa* and *Pocillopora damicornis* at Rottnest indicates the locally asexually produced recruits account for the maintenance of the populations, and that sexually produced recruits only rarely contribute.

Discussion

The research on benthic marine invertebrates at Rottnest Island can be considered from at least two points of view. The first is the development of our knowledge of the fauna of Rottnest Island, and the physical and biological processes which interact to produce the events and patterns we observe on these seashores. This development has been successful for two reasons. First, the studies have been of conspicuous, relatively large, sedentary or slow-moving animals. This approach allowed detailed and repeated observations on the same individuals as well as complete censuses of the adult populations. The second reason for success is that the studies at Rottnest Island have been quantitative and increasingly addressed to testing specified hypotheses for which particular kinds of information are purposely collected. The second point of view on marine biological studies at Rottnest Island depends on the descriptive background provided by the first, and also on a quantitative, hypothesis-testing approach, but is one of fundamental processes and general ideas in population and community biology, rather than the particular details of animals at Rottnest Island and communities.

In conclusion, or perhaps as a preface to the next phase of marine biological studies on Rottnest Island, there is an emerging pattern of environmental heterogeneity both in the processes involving sedentary adult animals on the shore, which can be studied directly, and in the processes involving the planktonic larval stages of these animals, which can only be studied indirectly. Even if processes both on the shore and in the plankton are deterministic, their interaction may lead to apparent chaos, in which the effect of environmental heterogeneity on the structure of populations and communities seems unpredictable. Predictability will come only from the study of this interation between processes.

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Immunological studies on the quokka

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[This paper is dedicated to the late Harry Waring and our PhD students.]

Abstract

A major advantage of studying marsupial immunology is that the marsupial pouch-young, at birth, are at a much earlier stage of development than eutherian young. Much of the work cited in this review concerns the cellular and humoral responses of marsupials from which the cervical and thoracic thymus glands had been surgically removed shortly after birth. Specific emphasis on the quokkas developed as they are representative of a property unique to the Phalangeroidea—the possession of two sets of thymus glands. A concept of the immunological recovery following total thymectomy is presented and it is concluded that marsupial and eutherian immunology are essentially similar and that the mammalian immune system must have been fully developed prior to marsupial and eutherian divergence.

Introduction

"The immune system is a diffuse organ assigned to monitor the identity of the body. Its basic constituents are lymphocytes and antibody molecules, both of which recognise foreign molecules and one anoher."[1]

After 20 years' study, 40 publications and four doctoral theses, the only general statements I am prepared to make are:

1. marsupial and eutherian immunology are essentially similar in all major aspects; and
2. the mammalian immune system must have been fully developed prior to marsupial and eutherian divergence.

Peripheral to and supporting the generalizations is a large body of data comprising interesting technical and conceptual studies initiated 20 years ago when the discipline of immunology was at an early stage of development. Today we have developed techniques of exquisite specificity and sensitivity that reveal function and activity not possible to visualize when we started in 1963. Rather than disregard the sound observations of the past, it is more useful to recognise imaginative and skilful work as it comes into perspective.

This short review pays tribute to many contributors, particularly the late Harry Waring. As I recall, the initial stimulus came from Sir MacFarlane Burnet when he suggested that "Waring and Stanley do something about that quokka thymus". We did. The first presentation of our quokka immunology research was made in 1966 at an international CIBA Foundation Symposium on the "Thymus—experimental and clinical studies" in honour of Burnet and coinciding with the 50th anniversary of the founding of the Hall Institute of Medical Research (Stanley *et al.* 1966). Reproduced here are the original figures showing the development of the cervical and thoracic thymus glands and their location.

The potential of marsupials as experimental models for immunological function was not fully appreciated until Miller (1962) demonstrated the critical role of the thymus gland in maturation of some immune responses in the mouse. From this initial observation there have developed the classical studies on T and

[1] After Jerne, N. K. (1973).—*The Immune System*, pp. 49-57. Freeman, San Francisco.